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EVOLUTION OF THE BASAL PLATES IN MONOCYCLIC CRINOIDEA CAMERATA. II

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PART II

2. CHANGES PRIMARILY MODIFYING THE RELATIONS OF PLATE CONTACT AND POSITION

The second series of changes, those which modify the primary position and relation of the basals and radials, will now be considered. These are: (*a*) reduction and compensating growth; (*b*) enlargement and compensating reduction; (*c*) plate division; (*d*) plate migration; (*e*) plate interpolation; and (*f*) anchylosis.

a) *Reduction and compensating growth.*—Reduction, or the diminution in size of a plate, may be either a function of the absorptive ameboid cells (see p. 502), or due to inhibited growth (atrophy). That is, the absorption of a fully outlined plate may take place, as in the absorption of the anal and oral plates in *Antedon*, or a continuous diminution in development to a former standard of size may result in the atrophy and final disappearance of a plate, as in the great reduction of the basals in *Pisocrinus quinquelobus*[1] and the disappearance of the first costal in some specimens of *Eucalyptocrinus rosaceus*[2] and *Alloprosallocrinus conicus*.[3] Atrophy in plate growth may be due either to plate contact, which inhibits the free branching and anastomosing type of development, or to some deep-seated morphological change. The simplest form of inhibition in plate development is that shown in the normal growth of plates after coming into mutual contact. It is the process which gives to the plates their polygonal outline and must not be considered a form of atrophy. Plate contact does, however, produce atrophy when the accelerated growth of one plate causes the reduction in size of some adjacent plate. This type of inhibition may be termed superficial atrophy, and is apparently the type just illustrated in the absorption of the first costal in *Alloprosallocrinus*. Atrophy of the other type is apparently the result of marked internal changes which appear on the exterior in the reduction of skeletal parts. This form of inhibition may be termed deep-seated atrophy, and is the type illustrated in the drawing together of the posterior radials in *Pterotocrinus* upon the reduction of the anal plate (Pl. III, No. 11.)

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[1] Ref. 5, p. 27.

[2] Ref. 28, p. 90, Pl. XI, Figs. 6, 7.

[3] In *Alloprosallocrinus conicus* the writer has found that the apparent anchylosis of the costal plates (see ref. 39, p. 407) is due to the complete reduction of the first costal.

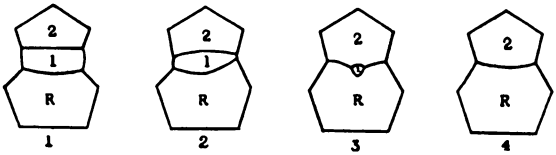

Fig. 6.—Figures showing the reduction of the first costal in *Alloprosallocrinus conicus:* 1 and 2, from specimen No. 9350; 2 and 3, from specimen No. 9357, in the University of Chicago collection.

With the decrease in diameter of a plate in a closed cycle there must be (1) a compensating increase in the diameter of some plate or plates in the same cycle, or (2) a decrease in diameter of some plate or plates of the apposed cycle; otherwise the symmetry of the cup will be distorted. The first principle is clearly demonstrated by the increase in diameter of the first interbrachial plates in *Amphoracrinus*[1] upon the gradual reduction of the proximal portion of the second anal plate. The second principle is clearly demonstrated in the reduction of the apposed compound basal and radial of *Zophocrinus*.[2]

This form of change might be confused with vertical plate-splitting followed by anchylosis of the parts to the adjacent plates if the change were a sudden mutation and no knowledge of the ontogenetic development obtainable; otherwise the phylogenetic succession would show the factors involved. If the reduction of a

[1] Ref. 32, p. 197.

[2] Ref. 6, p. 151.

plate in a closed cycle is asymmetrical, the growth of one of the laterally adjacent plates will be greater than that of the other, and will, on completion of the reduction, occupy the entire area of the missing plate. This process is shown nearing completion in the reduction of the antero-lateral radials in *Catillocrinus*,[1] and the consequent enlargement of the left posterior and anterior radials, and in *Mycocrinus*[2] in the reduction of the left anterior and dextro-lateral radials. In *Pisocrinus* the principle is diagrammatically shown in both basal and radial cycles, where, by the reduction of two basals and three radials, three basals, two radials, and the radianal are greatly enlarged (Fig. 7, Nos. 1–4).

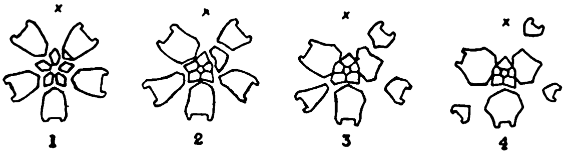

Fig. 7.—Diagrams illustrating reduction and compensating growth in *Pisocrinus:* 1, hypothetical, ancestral stage; 2–4, based upon specimens in the University of Chicago collection; x = position of first anal plate.

b) *Enlargement and compensating reduction.*—Plate enlargement, as we have seen, is due to the activity of the ameboid calciferous cells. In normal, symmetrical development the growth of the young plates is for a short time more rapid than that of the body wall, but upon plate contact the increased enlargement of both plates and body wall is theoretically balanced. If, however, a plate increases more rapidly than the adjacent plates, and is not controlled by the inhibiting influence of symmetrical development, and its accelerated growth is not compensated for by growth of the body wall, this growth must be compensated for in some other manner. Accelerated lateral increase of this type in a cycle plate demands then either (1) the decrease in diameter of some adjacent plate or plates in the same cycle or (2) the increase in diameter of some adjacent plate or plates in the apposed cycle and (3) distortion of the horizontal outline of the calyx or various combinations of the first two of these secondary developments may occur.

[1] Ref. 6, p. 149, Fig. LXII.

[2] Ref. 28, p. 110, Pl. 7, Fig. 4.

Accelerated increase of an interpolated plate between cycles or plate groups demands: (1) the decrease in size of some adjacent plate or plates, as in the decrease in size of the dextro-lateral radials in *Pisocrinus* (Fig. 7), upon enlargement of the radianal, or (2) distortion of the cup.

c) *Plate division.*—This process is the splitting of a plate into two (perhaps more) parts, either during or after the formation of the primary, formative cell group. Division of a cell group is due to cell separation, and may or may not be accompanied by cell division. Division of the plates when they are once formed is due to the action of the absorptive, ameboid cells. Division differs essentially from intercalation, in that a fundamentally distinct cell group is demanded for the interpolated plate. But no matter how division may take place, apparent evidences of division in the plates of fossil crinoids must be very carefully investigated before too much significance is attached to the opinion that division and not interpolation has taken place.

Division due to absorption is only known to occur during the absorption of the supporting rods in echinoid larvae,[1] and in the reduction of the radianal in *Antedon*.[2] Division or duplication is assumed by Bather[3] in the formation of the paired, proximal interbrachials in Actinocrinidae, yet all evidence from the work on crinoid larvae shows duplication and not division to be the process involved. Horizontal bisection is assumed by Bather[4] in ten genera of monocyclic Inadunata, not including those in which bisection of the right-posterior radial only occurs. However, when it is noted how closely the development and migration of the radianal in the larvae of modern crinoids parallels the development and migration of the radianal in the Flexibilia,[5] there is good reason to believe that bisection of the right-posterior radial has not occurred, but that the radianal and subradials are primary or interpolated (secondary) plates. Vertical splitting seemed beyond question in the formation of the compound, left-posterior radial in *Anomalocrinus*,[1] yet Springer[2] has shown it to be an abnormality, *due perhaps to plate fracture.*[3] There are, it is true, certain conditions surrounding apparent cases of plate division which lead us to believe that division and not interpolation has occurred. If, for example, two plates of the same cycle occupy the approximate area of one plate in that cycle, if they mutually fulfil the requirements of but one plate in that cycle, and if in the obliteration of the intervening suture a plate would be formed indistinguishable from the other four undivided plates in that cycle or from the morphologically undivided equivalent of that plate in a closely related ancestral genus, division would seem the only logical conclusion. But this conclusion is by no means proved. In the light of phylogenetic and ontogenetic development as ascertained from fossil crinoids division is very uncertain, for we cannot see the process taking place. Furthermore, if division had occurred anchylosis of the parts to the adjacent plates might take place and either complete absorption with compensating enlargement or migration would have to be called upon to explain the appearance of the new suture. Thus, no matter how carefully we attempt to ascertain the fact that division has occurred, the factor of interpolation will usually appear as an alternative. Only through careful observation, in modern larval development, of plates not destined to obliteration in the adult stage can this process be satisfactorily determined.

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[1] Ref. 34, pp. 349–54.

[2] Ref. 27, pp. 52, 53, Pl. 5, Fig. 11.

[3] Ref. 3, p. 34, fifth notice.

[4] Ref. 6, pp. 112, 144.

[5] Ref. 16, p. 332, 333.

d) *Plate migration.*—Any shifting which brings a plate, as a unit, into a new relation of contact and position with plates of the adjacent cycles, or of adjacent plates in the same series, may be termed a migration. For simplification in the discussion, the different types of migration may be broadly separated into two divisions: simple migrations, or those unattended by movements of the sarcode; and complex migrations, or those dependent upon movements of the sarcode. Of the simpler forms, three types occur: portional migration, cell-group migration, and simple plate migration.

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[1] Ref. 37, Part III, p. 221; ref. 40, p. 152.

[2] Ref. 32, p. 213.

[3] The italics are the writer's.

If the absorption or atrophy of one side of a plate and the growth on the opposite side are approximately equal, the plate would appear to be shifting as a whole, although actually stationary in part. This type of migration may be called portional migration, and is the type illustrated in the shifting forward of the postero-lateral basals in *Xenocrinus* and sometimes in *Eucalyptocrinus* and *Callicrinus*.

One form of cell-group migration involving the approximation and fusion of two groups into one would occur, if in the previous development of phylitic compression of characters anchylosis were to be carried back into the embryonic period. Thus, anchylosis which appeared as an adult character in early times might appear as an embryonic character in a later stage of development, and cause fusion of the formative cell groups. It is suggested that this type of fusion might be responsible for the interradial development of the two larger infrabasals in *Antedon*.[1] That cell groups as such may migrate in response to physiological stimuli from changed environment without any such evolutional change is also possible, and experimental evidence has been obtained to substantiate this hypothesis.[2]

Simple migration, after plate formation, without tortion or other movement of the sarcode, seems from the very nature of plate growth (see p. 501) to be impossible. This opinion is apparently substantiated by the system of migration of the anal plate in *Antedon*, and of the radianal in *Promachocrinus*[3] and *Hathrometra*,[4] and by the development of the posterior radials in *Antedon* upon the introduction of the anal. Equal spacing of the radials and the anal in the hexagonal stage of *Antedon* is not apparent; on the contrary, the space separating the postero-lateral and antero-lateral radials is much greater than that separating the postero-lateral radials and the anal. As the plates increase by branching and anastomosis, the adjacent margins of the anal and the postero-lateral radials meet and assume a finished appearance (Fig. 10) before the postero-lateral and antero-lateral radials meet. Forward shoving of the postero-lateral radials into this unoccupied area by growth pressure would be expected, but it does not occur. On the contrary, the posterior radials either assume an asymmetrical outline as in *Antedon*, most of the hexagonal Camerata (Pls. II-III), and many of the Fistulata, or the continued widening must be compensated for by accelerated growth of the sarcode in the posterior region. Since no better opportunity for simple plate migration could be conceived, and since it does not in this case occur, there is little reason for believing in its existence.

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[1] Ref. 8, pp. 288, 289.

[2] Ref. 26, p. 90.

[3] Ref. 16, p. 332.

[4] Ref. 24, pls. 8–12.

Complex migrations consist of plate shiftings induced by accelerated growth, tortion of the body wall, in either local or broad areas, which distorts the normal space and contact relation of plates. This form of migration is diagrammatically shown in the carrying up by elongation of the anal tube of the anal in *Antedon*, and of the radianal in *Promacocrinus* and *Hathrometra*. Where the anal and radianal, being more firmly attached to the viscera than to the adjacent plates, are bodily lifted out of the cup into the tegmen by the accelerated growth of the hind-gut, this process is the one which undoubtedly explains the migration of the radianal in all fossil crinoids. A more common form of complex migration, and one shown in many groups of crinoids, is that which results in the formation of biserial from uniserial ossicles in the arms.

e) *Plate interpolation.*—This process may be defined as the interpolation of some plate or plates, of primary or secondary derivation, between any plates forming the primitive crinoid cup and its appendages. It is one of the most common forms of evolution found in the crinoidea, and may be broadly separated into two groups: primary interpolation, or the development of primary or secondary plates *in situ* from a primary or secondary formative cell group; and secondary interpolation or migration. Only the first type need here be considered, as plate migration has already been discussed. Primary interpolation is the only known method by which additional stem ossicles appear; the new ossicles developing either between the base and the adjacent stem ossicles, as in the Inadunata and Camerata, or between other stem ossicles, as in the Flexibilia. In the development of cirri, primary interpolation is the rule, the interpolation taking place at the proximal end of the appendage. Here too belong the development of the perisomic[1] interbrachials, of the ambulacrals between the orals and interambulacrals, and of the peculiar plates appearing between the basal and radial cycles of *Acrocrinus*.[2] Interpolation in the basal cycle is known in but two genera. In *Sagenocrinus* and *Homalocrinus* the radianal is incorporated in the basal cycle, and in *Sagenocrinus* especially it assumes the appearance of a basal plate. Interpolation in the basal cycle, being well established in at least two instances, seems very rare, yet this may be due entirely to our lack of knowledge, for the evolution of the radianal plate in the Flexibilia leads one to believe that it appeared in its primitive state in the basal cycle.[3] A discussion of interpolation in the radial cycle has been purposely omitted in the preceding citations, as it belongs more properly in a discussion of the origin of the anal plate, where it will be fully considered.

It appears then that every cycle of plates excepting the infrabasals, and every series excepting the brachials, are affected by interpolation, and even in the brachial series Clark[4] has evidence which points strongly to interpolation. There is then a possibility that every plate cycle and series may be subject to interpolation, but this point is not of immediate consequence and need receive no further attention.

Interpolation in the calyx may demand (1) a reduction in some adjacent plate or plates of the same cycle or group, with or without oblique development of the plates,[5] as in the reduction of the posterior radials and oblique development of the radial cycle in *Antedon* upon interpolation of the anal plate; (2) an increase in diameter of some adjacent plate or plates in an apposed cycle or group, with or without trunkation, depending upon the alternating or superimposed position of the interpolated plate, as in the enlargement and trunkation of the posterior basal in some of the Camerata and Fistulata upon interpolation of the anal plate, and broadening of the radials without trunkation upon interpolation of interbrachials, as in many of the Camerata; (3) increase in the body wall, as is shown in the lengthening of the calyx of *Acrocrinus* upon interpolation of the extra plates between the basals and radials; (4) interpolation of an extra plate in an adjacent cycle or group to satisfy the demands of plate alternation; (5) deformation of the cup; (6) various combinations of the first four effects named.

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[1] Ref. 16, p. 339.

[2] Ref. 39, pp. 805–10, Pl. 53, Figs. 1–3, 4–9, and 10*a*, *b*.

[3] Ref. 31, p. 493, Pl. 5, Fig. 9.

[4] Ref. 13, p. 119.

[5] Oblique development is here used in reference to the displacement of either the proximal or distal ends of a plate, from the vertical axis of the cup and not from the planes of pentamerous symmetry.

f) Anchylosis.—The process of anchylosis is provisionally placed under this group of processes, because of its intimate association with certain modifications of plate contact and position which cast some doubt upon the propriety of assuming it to be a result and not the cause of those modifications. This fact is shown in the following section.

ANCHYLOSIS: ITS ANTECEDENTS AND CONSEQUENCES

I. ANCHYLOSIS AND REDUCTION

Anchylosis is the most potent factor operative in the obliteration of sutures, and while it has been discussed as a simple ontogenetic process, its antecedents and results have not been considered. The expression "reduction and anchylosis," so commonly used in the description of brachials, means anchylosis following and depending upon reduction, but whether or not this usage is morphologically correct is not clear to the writer. Anchylosis may take place without reduction, or reduction without anchylosis, although the former is not common. Anchylosis may perhaps be either preceded or followed by reduction, but the writer is inclined to believe that when anchylosis is preceded by reduction the reduction is phylogenetic, and that in ontogenetic development anchylosis is followed by reduction. That is, plates which will appear in the adult as a reduced anchylosed unit are in ontogenetic development up to the time of anchylosis the equivalent of the other plates in the same cycle or series, and with anchylosis inhibition of growth causes the reduction of the compound plate. This inhibition of growth may be due either to deep-seated atrophy in local areas or to local superficial atrophy.

The first change of interest in anchylosis of basals is the change of plate outline, from the pentagons through a heptagon to a hexagon. With lateral anchylosis of two basal plates, the pentagons of the basals are merged into a heptagon, with a re-entrant angle where the supported radial interlocks with the supporting compound plate. Upon further development, absorption decreases the angle of the radial plate, causing it to assume, first a lower angle, then a proximally convex outline, and finally, by complete absorption, a straight angle. At the same time, by increased deposition along the adjacent basal margin, the re-entrant angle of the heptagon is gradually filled, the filling comforming throughout with the reduction of the inserted angle. The final step is the change of the heptagon to a hexagon.

At some time either before, during, or after anchylosis, a remarkably persistent reduction of the compound plate or its component parts occurs. This reduction is parallel to the line of sutural closure, and is sometimes accompanied by reduction in the proximal diameter of the directly supported radial. From the principles set forth in the discussion of reduction and compensating enlargement, either compensating enlargement of the adjacent plates must take place or distortion follow the reduction. When only one pair of basals is anchylosed, as in the *Xenocrinus*, etc., and the *Calyptocrinidae*, the reduction is bilaterally symmetrical; the basals adjacent to the reduced plates are equally enlarged, and the reduction is apparently not due to deep-seated causes and affects only the basal plates and the proximal margin of the apposed radials (Pl. II, Nos. 2, 7). When two pairs of plates are anchylosed, as in the Stephanocrinidae, Pentremitidae, and Platycrinidae, the problem is not so simple, for on one side the compound basals are mutually apposed, and the intervening suture meets the center of the proximal margin of the radial. If the reduction of the compound basals is asymmetrical and occurs only on the sides opposed to the simple basal, no distortion in symmetry is necessitated. If, however, the reduction is symmetrical, there must be a distortion in symmetry of the cup, for there is no basal to enlarge where the compound plates are mutually opposed. In the Platycrinidae the reduction is asymmetrical, and is perhaps due to superficial atrophy.

The simple basal is in general symmetrically enlarged, and the base is occasionally a regular pentagon.

In the Stephanocrinidae and Pentremitidae the reduction of the compound basals is bilaterally symmetrical, and is usually accompanied by reduction of the radials directly supported by the compound plates. This reduction is compensated for on the anterior side by lateral growth of the simple basals and the radials obliquely supported by it. On the posterior side, however, distortion has taken place. If absorption had caused the reduction, either plate shoving or shrinkage of the sarcode would be necessary to keep the plates in contact; but plate shoving is apparently impossible, and shrinkage of the sarcode improbable. Upon comparison of the ornamentation in the reduced and unreduced radials in *Stephanocrinus*, another change seems to have taken place. The neural ridges of the reduced radials are fused, forming a single broad ridge, which apparently indicates that the underlying nerves are in closer relation than in the other radials. The reduction seems, then, to have been caused by the inhibition of lateral expansion in the sarcode in the reduced areas, and not to absorption, and is a very good example of deep-seated atrophy. In the three-basaled, hexagonal Camerata, anchylosis and reduction of the basals are complicated by the appearance of the anal plate, and cannot now be considered.

2. DELAYED ANCHYLOSIS

In many genera, especially of the hexagonal Camerata, anchylosis takes place at such an early period in development that no trace of the immature forms with unanchylosed basals is preserved. The only hope, then, of locating the missing suture is by delayed anchylosis, or characteristics of ornamentation. Ornamentation has, however, received so little study, and the subject is so broad, that the writer cannot at present give it adequate consideration. Examples of delayed anchylosis, however, are not unknown, and a number of cases will be cited in the latter part of this paper. Delayed anchylosis is simply a nascent stage of anchylosis, due to the inhibition of activity in the ameboid calciferous cells. It may appear in the form of internal or external grooves, or in its completeness as an unchanged suture. In the latter case, it is in the Camerata always accompanied by the inserted angle of the apposed radial. In the pentagonal Camerata the reappearance of a suture or group of sutures would unhesitatingly be described as cases of delayed anchylosis. In the hexagonal forms, however, doubts might arise concerning the reappearance of the anterior suture in the three-basaled genera and of the right-anterior suture in the two-basaled genera, since such reappearance would, according to Wachsmuth and Springer, indicate the presence of six basal plates (pp. 492–93). There might also be some question as to whether these reappearances are due to delayed anchylosis or resorption; but until more light can be thrown upon the problem of sutural reappearance by reabsorption of the intrasutural deposit, these abnormalities may well be ascribed to delayed anchylosis.

3. ANCHYLOSIS AND THE PHYLOGENETIC REAPPEARANCE OF SUTURES

Anchylosis of the basals, as far as we now know, is an ontogenetically repetitive process, confined to plates and not taking place as a result of cell-group fusion. The basal sutures are always present in ontogenetic development, and constitute phylogenetically a plane of weakness in the compound plate. This is apparently not true of the infrabasals, at least in modern forms, as is shown in the interradial development of two of the infrabasals in the embryo of *Antedon*. Atavistic reappearance of sutures, by delayed anchylosis, is a possibility, but the cenogenic or phylogenic reappearance of a suture lost through anchylosis is another question. The skeleton of the Echinoderm is deposited in the midst of living tissue and remains under the full control of the ordinary processes of growth, reabsorption, and modification by living tissue.[1] The partial or total absorption of plates, the shifting of sutures, and the reabsorption and modification of the basals in the formation of the centro-dorsal are sufficient evidence of this statement. It seems possible, then, that under the conditions of physiological disturbance (loss of vitality) common in the paracme of development,[2] failure of anchylosis or reabsorption of the intrasutural deposit might take place, and the sutures reappear as phylogenetic characters; but we have no evidence of such a reversion, and, until such evidence is brought forward, theories of descent demanding the reappearance of lost sutures should be carefully scrutinized.

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[1] Ref. 7, p. 350.

[2] *Ibid.*, p. 350.

DEVELOPMENT OF THE INTESTINE AND THE CONSEQUENT ZONES OF POTENTIAL WIDENING

"In all the Echinoderm classes it is the digestive tube that controls any departure from pentamerous radial symmetry." This statement by Clark[1] may perhaps be too sweeping in extent, especially when we consider the potency of atrophy and compensating hypertrophy (p. 533) in distorting symmetry; but the fact that the digestive tube is one of the most powerful factors in distorting symmetry cannot be too strongly emphasized. The most striking and therefore the most widely known effect of this power is that shown in the various distortions of the mouth and ambulacral grooves by excessive growth of the hind-gut. These tegminal distortions have been so frequently described that there is no necessity of reviewing them here; distortions produced by the intestine in the basal and radial cycles have, however, received too little attention.

In the development of the digestive system in *Antedon* the gastric sack is elongated horizontally into a form somewhat resembling the human stomach, having a large end into which the funnel-shaped oesophagus opens, and a small end with a caecal termination, which is the potential intestine. Upon further development the intestine is also horizontally prolonged, and coils to the right, around the stomach, in the space left for it by the enlargement of the calyx;[2] before the coil is completed, however, the anal appears and the intestine directs itself toward that plate. The pressure exerted by the intestine upon the anal tends to keep separated the posterior radials and prevents the right-posterior radial from encroaching upon the anal.[3] Soon, however, the intestine turns upward and carries the anal with it into the tegmen. The thrust exerted by the outward growth of the intestine which displaces the anal and also the radianal (see p. 538) must not be considered as a gentle pressure, nor the displacement of these plates as a gentle process, due only to their much closer association with the intestine than with the surrounding plates.[1] The outward push of the intestine is in proportion to the strength of the calyx walls a powerful force, capable of inhibiting plate growth and of greatly distorting the relations of plate contact and position.

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[1] Ref. 16, p. 152.

[2] Ref. 12, pp. 227–28.

[3] Radianal. See Ref. 16, p. 333.

In the recent works of Springer and Clark attention has been called repeatedly to the remarkable parallel between the ontogenetic migrations of the radianal in modern crinoids and its phylogenetic migration in fossil forms. Since the migration of the radianal in recent forms is caused directly from its intimate association with the hind-gut in its upward growth, there can be no doubt that such an association existed in the ancient crinoids, and that the tendency for shifting the radianal gradually increased and the association became so firmly established that the radianal is now completely withdrawn from the cup in individual development.

The radianal in the early Flexibilia is incorporated in the basal cycle below the right-posterior radial, and probably appeared in that position in the ancestors of the Flexibilia.[2] The outward push of the developing intestine was then directed obliquely to the right against the radianal and in the succeeding stages shoved and pulled this plate upward and to the right into the posterior interradius and out of the cup. Furthermore, in *Sagenocrinus*[3] it permitted such an enlargement of the radianal that the right margin of the posterior basal was shoved to the center of the posterior interray. This change is of especial interest in the study of basal plate evolution, as it shows one method of obtaining a posteriorly directed basal suture, such as is exhibited in all genera of Camerata having a hexagonal, tripartite base.

This apparent digression from the subject of basal plate evolution in the Camerata—a group in which, as far as we now know, a radianal plate never appeared—is for the purpose of bringing clearly to mind the powerful effect of the growing intestine and the presence of zones of potential weakness in the calyx. These zones of weakness lie along the posterior interradius in the radial cycle and along the right-posterior radius in the basal cycle, and it is to the latter zone that especial attention is called. Wachsmuth and Springer have noted this zone of potentiality in but one instance (description of Fig. I, No. 7, of this paper), although it seems the only zone of potentiality in the basal cycle which can logically be accounted for. Pressure from the end of the developing hind-gut must from the necessity of its position be directed obliquely to the right against the posterior interradius, and any lateral pressure of the gut must be directed against the right side of the calyx, the two combining to shove the right side outward and away from the left side. Thus the stress produced by this shove would naturally fall along the right-posterior basal suture, as this is the nearest suture or plane of expansion adjacent to the posterior interradius within the zone of pressure exerted by the hind-gut.

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[1] Ref. 11, p. 732.

[2] Ref. 31, p. 439, Pl. V, Fig. 9.

[3] *Ibid.*, Pl. VII, Fig. 18.

ORIGIN OF THE ANAL PLATE

Comparison of the cup and tegminal structures in the Batocrinidae and Platycrinidae shows that a very long period of time must have elapsed, or very rapid evolution have taken place, before such a highly specialized form as *Tanaocrinus* could have originated from any of the early Platycrinidae. Since *Tanaocrinus* is an early Silurian (Richmond) genus, relationship can be established with the Platycrinidae only through Ordovician or pre-Ordovician ancestors; therefore, if *Tanaocrinus* is related to the Platycrinidae, it must have been derived from a form having a simple, pentagonal, five-basal cup. The primary step in the evolution of this form into *Tanaocrinus* would be the introduction of the anal plate into the radial cycle, thus giving to the cup its hexagonal outline, and inducing in the basal-plate cycle a remarkable series of modifications. The questions then arise: How do we know that the anal was a secondary and not a primary plate? At what period in the ontogenetic development of the Camerata was it interpolated in the radial cycle? Where did it originate? And what changes followed its interpolation? It is generally agreed that the anal plate in the hexagonal Camerata is of secondary origin. If this is true, the statement just made concerning the ancestry of *Tanaocrinus* is undeniable, for by eliminating the secondary plates of that genus and restoring the orals an ideal larval or ancestral form will appear. If, however, the anal plate is a primary plate in the radial cycle, a different line of descent is indicated.

In the ontogenetic development of the skeleton in the living *Antedon* the anal plate is interpolated after the basals and orals have formed closed cycles, and before the radials are laterally in contact. As the anal expands by lateral and proximal growth, it comes into contact with the posterior radials and the posterior basal; but this happens before the distal margins of the basals are completed and while the radials are still separated from each other. Since growth in the anal plate and the posterior radials does not cease upon their coming into contact, shoving of the posterior radials in the direction of the unoccupied lateral areas might be expected. This, however, does not occur. On the contrary, the crowding results in a partial inhibition of growth in the apposed margins, and a marked asymmetry results in the outline of the posterior radials, especially in the right-posterior radial. If comparison is now made between *Antedon* in this stage of development and the early Camerata having a hexagonal base, a striking similarity is seen in the development of the basals, radials, and the posterior side of the calyx. The posterior radials in both forms are asymmetrical and narrower than the anterior radials, and the asymmetry is due to the diminution of the posterior side of the plates, the distance between the center of the radial facet and the plate margin being less in the posterior half than in the anterior half. If comparison is then made between the relative position of axial lobes and radial plates in pentagonal and hexagonal Camerata, a further distortion is noted in the hexagonal forms. The lobes of the canal in the pentagonal forms occupy an interradial position, while either two or three of the lobes in the hexagonal forms occupy a radial position. These facts show that there is a distorting factor present in the posterior side of the cup. When it is considered that pentamerous symmetry is the rule in Echinoderms, and that sutural symmetry based upon the hexamerous plan only appears in the basal cycle with the appearance of the posteriorly directed basal suture, there seems to be no other alternative than that the anal plate is the distorting factor, and that it has developed secondarily in the radial cycle, or has migrated into that position.

The origin of the anal plate is as yet an unsettled question, but there are several possibilities which may well be considered. It may have originated as a secondary plate in either the basal or oral cycle. It may have developed as one of a brachial series, or an interbrachial cycle, or it may have originated as a separate plate in the radial cycle. Origin in the basal or oral cycles is clearly out of the question, for we know of no plates in either cycle from which it could have originated. Assumption of origin as a brachial, which is Bather's explanation for the origin of the anal plate in the Fistulata,[1] is without foundation in the Camerata.

Origin as one of an interbrachial series of the ordinary type is also improbable, for although these interbrachials are present in *Tanaocrinus*, *Xenocrinus*, and *Compsocrinus*, they are clearly formed at a later stage of development. Origin as a first interbrachial, that is, one of an interbrachial series interpolated between the radial plates, has been seriously considered by Carpenter[2] in a comparison of *Xenocrinus*, and some of the dicyclic Camerata, with *Antedon* and *Thaumatocrinus renovatus;* and while such a cycle may have existed and the lateral plates have atrophied, there has been found no record of such a cycle in the monocyclic Camerata. This, however, does not preclude the idea that the anal series may have been so interpolated, and that the lateral plates which appear in some of the dicyclic Camerata have been the result of reduplication.[3] Let us examine the ornamentation in the anal series of *Compsocrinus* and *Xenocrinus*, and see if this may not throw some light upon the question. Bather, in calling attention to the anal ridge in the Reteocrinidae, *Glyptocrinus*, etc., says, "The *anal* ridge is connected with the ridges that unite the posterior basal to the right- and left-posterior radials, and this indicates that an axial cord passed up it to govern the motions of the anal tube."[4] That this ridge does so indicate the presence of an anal nerve seems beyond question, for in comparing the ornamentation in *Xenocrinus* and *Compsocrinus* with the nervous system of

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[1] Ref. 4, pp. 319–31.

[2] Ref. 10, pp. 38–46.

[3] Ref. 16, p. 338.

[4] Ref. 6, p. 119.

Thaumatocrinus a striking similarity is discovered. In *Thaumatocrinus* the interradial arms are innervated by secondary branches of the axial cord, which originate slightly above the point of bifurcation of the basal cord, quickly join, and pass up the interradial arms, while the main branches pass up to the radials (Fig. 7, No. 2). In *Xenocrinus* and *Compsocrinus* (Fig. 8, No. 1) the anal nerve ridge arises at the point of bifurcation of the axial trunk ridges in the posterior basal, and there can be little doubt that the branching of the underlying nerves took place in the same manner as they do in *Thaumatocrinus.* The parallel here is so close that the writer was at first inclined to the belief that the interpolation of the anal series in the Camerata is of the same type as the interpolation of the interradial arms in *Thaumatocrinus.* In *Thaumatocrinus*[1] the "interradial" radials appear very early in the ontogenetic development as narrow plates separating the radials and gradually increase to the size of the true radials. An objection to this form of development has been stated by Bather, on the ground that no primitive genera have been found in which the anal plate appears as a narrow linear plate.[2] This objection, however, is not formidable, for the change may have been a discontinuous mutation, or may have taken place during periods of retreat of the sea. Ulrich believes that most mutations have so taken place, for he says in the "Revision of the Paleozoic Systems": " . . . . almost invariably we deal with the nearly finished product of a process of mutation that was begun and established before the new phase invaded areas now accessible to the student of fossil faunas."[3]

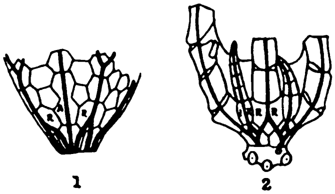

FIG. 8.—Diagram showing the course of the radial and anal ridges in *Compsocrinus* and the branching of the nerves in *Thaumatocrinus:* 1, *Compsocrinus harrisi* (based upon Wachsmuth and Springer); 2, *Thaumatocrinus renovatus* (after Carpenter); course of nerves based upon dissection by the writer.

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[1] See Ref. 16, p. 337.

[2] Ref. 3, fifth notice, p. 37.

[3] Ref. 36, pp. 498–501.

The logical sequence of events based upon the *Thaumatocrinus* theory would be the interpolation of the anal plate in the radial cycle and serial development of the succeeding anals. But when this sequence of events is applied to the pentamerous, monocyclic Camerata difficulty is immediately encountered. Either these forms have lost their true anal plate and the anal now appearing in them is the homologue of the second anal in the hexagonal Camerata, or they have developed along a different line of evolution from the hexagonal forms. But before taking up these questions let us examine this theory of interpolation more closely.

Stratigraphically the pentamerous base precedes the hexamerous base, and it seems scarcely possible that a hexagonal form which could give rise to both *Glyptocrinus* and *Tanaocrinus* could have been living in the ocean basin during pre-Ordovician and Ordovician times, and that only those forms having lost the anal plate should have migrated into the epicontinental seas during the Ordovician, while those having the anal plate were withheld until Silurian (Richmond) times. This is apparently carrying the theory of selective action too far to be believed. Again, the embryological evidence shown in *Thaumatocrinus* may not be reliable. We have noted that the radianal in *Promacocrinus* originates to the left of the right-posterior radial; furthermore, we know that the radianal appears in the more primitive crinoids in a subradial position. There has been not only a progressive upward shifting of the radianal in these groups, but there has been apparently a progressively upward shifting of its point of origin. Embryology does not repeat all the ancestral characteristics step by step and then eliminate them in a different fashion in producing the various genera and species; certain characters which are gradually being eliminated phylogenetically are probably, in Crinoidea, the result of a progressively increasing inhibition of plate development in the larva, which ends in the complete obliteration of the plate.[1] Since embryology does not repeat all the ancestral stages, and does in this case permit of changes in the position of origin of a plate, there is a possibility that the "interradial" radials in *Thaumatocrinus* did not originate in the position in which they now originate, and too much dependence should not be placed upon this character. The evidence presented by fossils is fixed, although often wrongly interpreted, and until stronger evidence is submitted it is well to hold closely to that presented in the stratigraphic succession.

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[1] For a more complete discussion of this phase of development based upon a wide series of observations, see Ref. 23, Chap. III, "Recapitulation."

Stratigraphically the pentamerous base preceded the hexamerous base, and when we consider with this the evolution of the two-basaled, hexagonal Camerata, a more logical theory of development for the anal plate is presented. In this short-lived group we have a very rapid evolution from some platycrinid stock. The anal plate in *Platycrinus* originates in the posterior interray between the distal margins of the radial plates, while the anal plate in *Dichocrinus* projects above the level of the radials and costals and bends sharply inward toward the anal tube; its distal portion is reduced, and, if it were separated from the enlarged proximal portion and slightly modified, could not be distinguished from the anal in *Platycrinus*. Enlargement and downward growth of the anal seems then to have occurred, and a different theory is offered for the interpolation of the anal plate.

This theory for the appearance of the anal plate is, then, that the anal plate is of secondary derivation; that it was interpolated phylogenetically after closure of the radial cycle, but ontogenetically after the basal had formed a closed cycle and before the radials had come into contact. The cup in this stage of development is in a flexible condition, and readjustments can readily be made. Development of the anal plate in this position requires no true migration to come into contact with the posterior basal; portional migration, or proximal growth with distal inhibition in the younger stages, will produce the *Tanaocrinus* type of anal, while distal growth alone is necessary to produce the *Glyptocrinus* type of anal. The stimulus which kept the radials apart and permitted this downward growth of the anal plate was the demand for room on the part of an enlarging hind-gut, and it is this stimulus which has caused some of the most remarkable changes in crinoid evolution. Additional plates in the anal series were probably added as needed, for protection of the anal tube, and no slipping downward of a completed series of anals is required. In considering this change we must remember that we are not dealing with a completed model in which the plates are of fixed and unchangeable size, and in which every change of plate position must be accompanied by an entire readjustment of the adjacent plates; we are dealing with a growing organism in which there is a certain amount of flexibility in adjustment by plate growth.

If this theory for the interpolation of the anal plate is correct, the first anal plates of *Glyptocrinus*, *Platycrinus*, and *Dichocrinus* are homologous; and in further developing the theory for the evolution of basal plates this view will be followed.

[*To be concluded*]